Parallel shifts in flight-height associated with altitude across incipient *Heliconius* species

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Abstract

Vertical gradients in microclimate, resource availability and interspecific interactions are thought to underly stratification patterns in tropical insect communities. However, only a few studies have explored the adaptive significance of vertical space use during early population divergence. We analysed flight-height variation across speciation events in *Heliconius* butterflies representing parallel instances of divergence between low and high-altitude populations. We measured flight-height in wild *H. erato venus* and *H. chestertonii*, lowland and mountain specialists respectively, and found that *H. chestertonii* is consistently flies at a lower height. We compared these data with previously published results for *H. e. cyrbia* and *H. himera,* the latter of which flies lower and like *H. chestertonii*, recently colonised high-altitude, dry forests. We provide evidence that these repeated trends are largely driven by shared sources of selection across equivalent environments, producing similar trait-shifts in *H. himera* and *H. chestertonii*. Although our results imply a signature of local adaptation, we did not find an association between resource distribution and flight-height in *H. e. venus* and *H. chestertonii*. We discuss how these results may be explained by variation in forest structure and the microclimate. Overall, our findings underscore the importance of behavioural adjustments during early divergence mediated by altitude-shifts.

Key words

Heliconius, local adaptation, flight-height, parallel evolution.

Introduction

The steep environmental gradients that characterise the upper and lower vegetation layers of tropical forests are a key factor determining species abundance and diversity [1-5]. In arthropods, particular species are consistently found in some vertical strata while being less common in others due to variation in abiotic conditions, behaviour, and the distribution of resources [6, 7]. For example, fruit-feeding and nectar-feeding butterflies, respectively decrease and increase in abundance towards the canopy, ostensibly tracking their food sources [8-10]. This has broad implications for the structure of communities, with consequences for wider trophic interactions [11, 12].

Comparatively, less is known about vertical segregation occurring between closely related populations. Only a handful of studies have examined divergence in the use of vertical space at this level, but these provide a range of evidence implicating flight differences in early divergence. For instance, closely related *Heliconius* species that that fly in separate vertical strata have different wing morphologies [13]. Similarly, the Nymphalid *Archaeopreponae demophon* includes coexisting canopy and understory populations with independent demographic dynamics and low levels of gene-flow, despite their similarity and proximity [14]. Divergence in resource use, combined with changes in larval behaviour, have also been linked to species divergence in *Colobura dirce* [15], which can be split into two separate species based on differences between their larvae: *C. annulata* are gregarious and feed on mature, canopy *Cecropia* leaves while *C. dirce* are solitary and consume understory saplings [15]. These examples suggest a role of vertical space in local adaptation, but the underlying mechanisms remain unclear.

Recently, heritable flight-height differences were demonstrated between the *Heliconius* species *H. e. cyrbia* and *H. himera* [16], which are distributed along a gradient from wet, low-altitude to dry, high-altitude forests, with a narrow zone of overlap where the two hybridise [17]. This correlates with the distribution of resources in their habitats such that *H. himera* flies lower than *H. e. cyrbia*, tracking the height of hostplants and flowers that are positioned lower at high-altitude [16]. This pattern may result from divergent ecological selection maximising hostplant encounter rates and foraging efficiency across forests with different structure, potentially contributing, alongside other factors [18-21], to the evolution of reproductive isolation.

In the western slope of the Colombian Cordillera Occidental, *H. e. venus* and *H. chestertonii* are distributed along a similar ecological gradient (Rivas-Sánchez et al., in press) (Figure 1 d-e). *H. e. venus* occupies wet forests at sea level, whereas its close relative *H. chestertonii* lives in drier, scrub forests in the mountains [22, 23]. Because *H. chestertoniii* is spatially and genetically independent from, but ecologically comparable to *H. himera*, it can be studied as a convenient replica to explore the relationship between vertical segregation and divergence during the early stages of speciation. Here, we tested whether *H. e. venus* and *H. chestertonii* fly at different heights and if this correlates with the location of larval and adult-stage resources in their respective habitats. Under the assumption that flight-height patterns constitute adaptive traits, we predicted that flight-height variation between *H. e. venus* and *H. chestertonii* would mirror that between their ecological equivalents *H. e. cyrbia* and *H. himera.*

Methods

i) Habitat characterisation

We investigated *Heliconius* butterflies in four sites representing the habitats of *H. e. venus* (Buenaventura, N 03º50'0.04" W77º15'45.1" and La Barra, N 03°57.558420 W 77°22.705080) and *H. chestertonii* (Montañitas N 03º40'36.3" W 76º31'19.4" and El Saladito N 03º29'11.5" W 76º36'39.8") in January 2021. At each of these sites, we characterised the local forest structure by measuring the trunk diameter at breast height (m) and the average distance (m) between neighbouring trees of common tree species. Additionally, we used clinometers and measuring tapes to estimate the height (m) of the canopy, the understory, and the shrubs in each site.

ii) Vertical distribution of resources

We explored whether the distribution of adult and larval resources differed between habitats. To do this, we measured the height (m) of all the *Passiflora* (Passifloraceae) hostplants that were visually identified along the trails used to collect butterflies. These plants were subsequently identified to the species level [24, 25] and filtered so that our dataset consisted exclusively of species known to be used by butterflies in the *erato* complex [26, 27], to which our focal species belong. We also measured the height (m) of the flowering plants that adult butterflies were observed feeding from at least once. Note that these methods differ slightly from Dell'Aglio, Mena [16], where plants were identified by following butterflies until they landed on a flower or hostplant. Due to the trail and forest structure, this approach was not possible here.

iii) Patterns of flight-height divergence

We measured the flight-height (m) of *H. e. venus* (n=33) and *H. chestertonii* (n=39) at the point where individuals were first encountered using measuring tapes. The butterflies were collected, sexed and marked, ensuring no repeated observations. To quantify levels of parallelism in flight-height with butterflies from an independent, ecologically equivalent pair, we included flight-height measures of *H. e. cyrbia* (n=78) and *H. himera* (n=86) in our dataset, available in Dell'Aglio, Mena [16].

iv) Statistical analyses

To test for significant differences in the diameter at the breast height, the average distance between neighbouring trees, and the height of different forest layers between habitats, we used Wilcoxon rank sum tests implemented in R [28]. We also modelled variation in the height of hostplants and flowers separately using linear mixed-effect models (implemented in *lme4* [29]) with "habitat" as a fixed factor and "site" as a random effect. This was followed by Wald χ^2 tests (implemented with the *Anova* function in the package *CAR* [30]). To analyse flight in *H. e. venus* and *H. chestertonii*, we used linear-mixed models where variation in flight-height was explained by the fixed factors "subspecies" and "sex", as well as their interaction and the random factor "site". We subsequently used the *drop1* function in base R to

remove model terms unless their deletion was detectable via likelihood tests. This resulted in a reduced model with subspecies as the only main effect.

Finally, to test for parallel shifts in flight-height across independent divergence events, we used a variance partitioning approach [31] combining data on *H. e. venus*, *H. chestertonii*, *H. e. cyrbia* and *H. himera*. In detail, in our model we included the main factors "habitat" (similarity of selection regimes across independent divergence events) and "locality" (variation in flight-height that responds to the unique properties of each divergence), as well as a "habitat*locality" interaction term (inconsistency in magnitude and/or direction of divergence patterns of the two pairs of species). We assessed the significance of each of these terms via likelihood (*drop* 1 function) and Wald χ^2 tests between alternative models with and without specific factors. We then estimated semi-partial R^2 coefficients (*r2beta* function, Kenward Roger method in the R package r2glmm [32]) in our final model, providing a rough approximation of the proportion of variance explained by each term.

Results

The habitats of *H. e. venus* and *H. chestertonii* broadly differed (Figure 1a-c). In particular, the trunk diameter at the breast height (W=32, $p<0.05$) and the distance between neighbouring trees (W=15, $p<0.01$) were both significantly higher in the habitat of *H. e. venus*. In addition, the height of the canopy and the shrubs forest layers were not significantly different between the two forest types, but the understory layer was significantly shorter in the habitat of *H. chestertonii* (W=30, $p<0.01$). in contrast, we were unable to confirm significant differences in the vertical distribution of hostplants (n= 37, χ_1^2=0.3949; p=0.5297) or flower resources (n=107, χ_1^2=0.0096; p=0.9219; Figure 2a-b) between different habitats.

On average, *H. chestertonii* flew ~0.5 m lower than *H. e. venus* (n=74, χ_1^2=8.8601; $p< 0.01$; Figure 2c) suggesting a parallel shift in flight behaviour occurred in *H. chestertonii* and *H. himera*. Indeed, in our full model combining data from *H. e. venus*, *H. chestertonii*, *H. e. cyrbia* and *H. himera*, the proportion of variance attributable to "habitat" was higher than the attributable to differences in localities or habitat*locality interactions (Table 1). Moreover, likelihood ratio comparisons between alternative models showed that the effect of "habitat" was significant (n=240, χ_1^2=21.725; $p<0.001$) but not the effect of "locality" nor the interaction between them, suggesting a close correspondence between the patterns of divergence in flight-height in *H. e. venus*-*H. chestertonii* and *H. e. cyrbia*-*H. himera* (Figure 2d). In our reduced model with "habitat" as the only main factor, "habitat" explained more than half of the variation flight-height between species (Table 1). .

Discussion

We leveraged two separate events of evolutionary divergence across ecologically equivalent *Heliconius* taxa pairs in Colombia and Ecuador to explore local adaptation in the context of altitude shifts. We demonstrate that the mountain specialist *H. chestertonii* flies at a lower height compared to its ancestral-proxy, low-altitude population, *H. e. venus*, closely mirroring a pattern formerly reported for *H. himera* (high-altitude) and *H. e. cyrbia* (low-altitude) [16]. This strongly implies a role for

shared sources of divergent selection across habitat types driving local adaptation in flight-height. However, we were not able to formally link shifts in flight-height in *H. chestertoniini* to the distribution of plant resources.

Adaptation can be inferred when phenotypic differentiation takes place in parallel across replicate populations from similar environments [31, 33, 34]. The derived populations of *H. chestertonii* and *H. himera* independently colonised similar mountainous habitats in the Eastern Andes, as evidenced from genomic data which isolates these species in separate genetic clusters [22, 35]. Although we measured flight height in wild individuals, the differences we found may be heritable, as demonstrated in common garden experiments with *H. e. cyrbia* and *H. e. himera* [16], and therefore subject to selection. Indeed, our tests for parallelism suggest these independent shifts in flying behaviour are largely driven by shared sources of divergent selection rather than stochastic evolutionary processes (e.g., genetic drift or gene-flow) [31, 34, 36] and might thus constitute a signature of repeated local adaptation (e. g. [37-41]).

In contrast to *H. e. cyrbia* and *H. himera* [16], we found no evidence for an association between flight-height and the distribution of larval or adult resources in *H. e. venus* or *H. chestertonii*. In other species, such correlations have been interpreted as evidence that butterflies fly at a height that maximises encounter rates with resources [8, 9, 42, 43]. Passion vines are strongly influenced by the forest architecture because they rely on multiple plant species for structural support [25]. *P. auriculata* was the only suitable hostplant in the *H. e. venus* habitat, whereas we found both *P. biflora* and *P. suberosa* in the *H. chestertonii* habitat. These three species belong to the same subgenus (*Decaloba*) and grow to modest dimensions [24], likely explaining their similar heights in the wild. This lack of differentiation conflicts with the hypothesis that flight height differences are a result of selection to maximise foraging and oviposition opportunities. Interestingly, in the lower altitude *H. e. venus* La Barra site, we found a few plants of a fourth species, *P. micropetala,* which grow up to 6 m tall. We did not include these plants in our analyses (although their inclusion does not qualitatively effect our results due to small sample size), as it is unknown if *H. erato* uses *P. micropetala*. Nevertheless, *P. micropetala* is a very near relative to *P. biflora* [24] and *Heliconius erato* are known to switch hosts seasonally when their preferred hostplant is depleted [44-47]. Regardless, the presence of these taller *Passiflora* in the *H. e. venus* habitat resonates with the idea that the lowland, forest understory offers support for taller *Passiflora* [16, 25]. Further studies could confirm whether *P. micropetala* is indeed used by *H. e. venus*, which may relate to the flight-height differences we observed in respect to *H. chestertonii*.

In Colombia, the structure of high and low-altitude forests differs such that the mountainous habitat of *H. chestertonii* has generally shorter trees at higher densities. This high-altitude forest is also colder and drier (~ 7 °C and ~3% RH differences) (Rivas et al., in press). These differences mirror those between the habitats of *H. e. cyrbia* and *H. himera* [16] and may potentially result in alternative sources of divergent selection across both pairs of taxa. For instance, oviposition behaviour can be affected by microclimatic conditions [48, 49]. Using dummy models, Merckx, Van Dongen [50] also showed that the woodland butterfly, *Pararge aegeria*, can warm up faster when ambient temperatures are higher, and experiences less convective

cooling at lower flight-heights and in forests with a more sheltered structure. Pupation height is also partly driven by desiccation avoidance, which is lower closer to the ground [51]. It is therefore plausible that the butterflies in our study are flight-height adjusted to compensate for habitat-differences that affect temperature-dependent traits, rather than to match resource availability.

In conclusion, we showed that two derived mountain specialist *Heliconius* butterflies have independently evolved flight behaviours via trait-shifts that are similar in magnitude and direction, suggesting underlying repeated local adaptations in forests at different elevations. In Colombia, this pattern does not appear to be driven by differences in the vertical distribution of hostplants or nectar and pollen rich flowers. We suggest that these parallel differences may instead relate to effects of variable microclimatic conditions between forest types. These results add to a limited list of studies exploring potential mechanisms explaining flight-height differences between closely related insect taxa in the tropics.

Figures and table

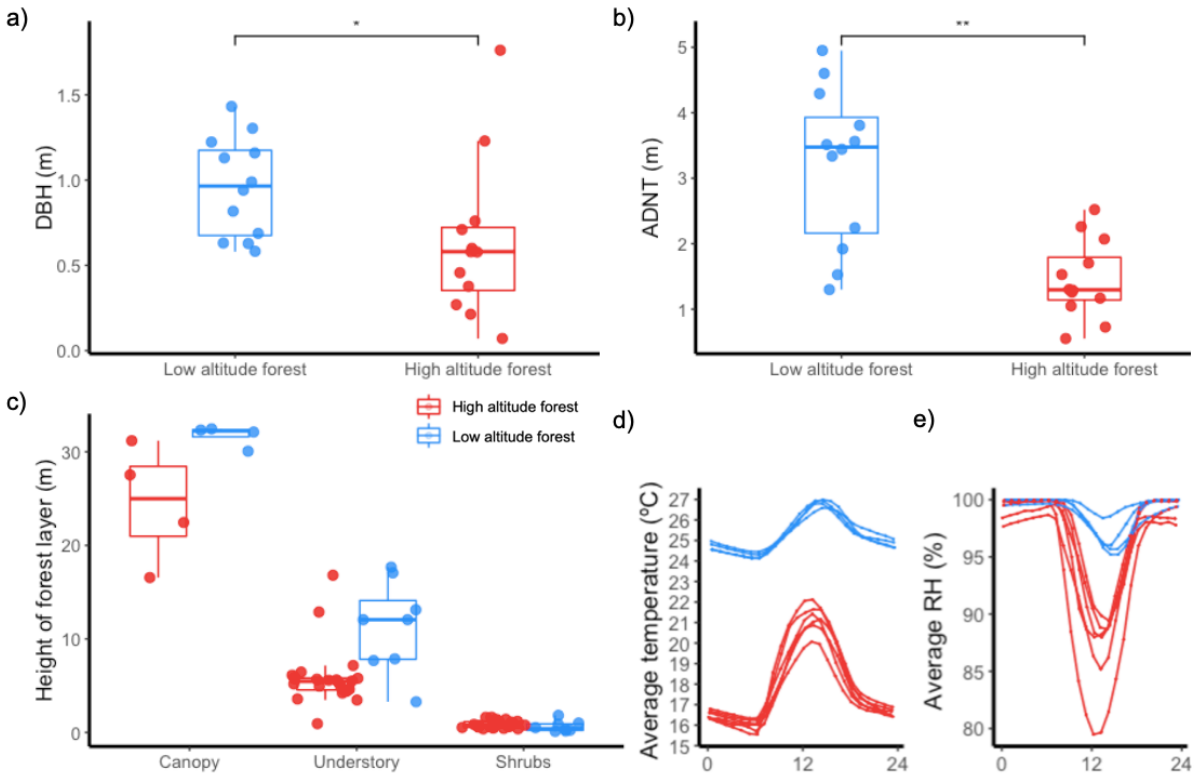

Figure 1. Broad characteristics of low-altitude (blue) and high-altitude (red) habitats. Comparison of a) diameter at the breast height (DBH), b) average distance between neighbouring trees (ADNT), c) canopy, understory, and shrubs heights, d) average temperature and e) average relative humidity throughout the day. In a-c), box plots show the median and upper and lower quartiles, each point is an individual measure. Asterisks convey significance levels of comparisons (Wilcoxon test). NS, not

significant. * p < 0.05. ** p < 0.01. *** P < 0.001. In d-e) (modified from Rivas *et al* 2022 in press), each line represents microclimate data point recorded by a data logger deployed in low-altitude (blue) or high-altitude (red) forest.

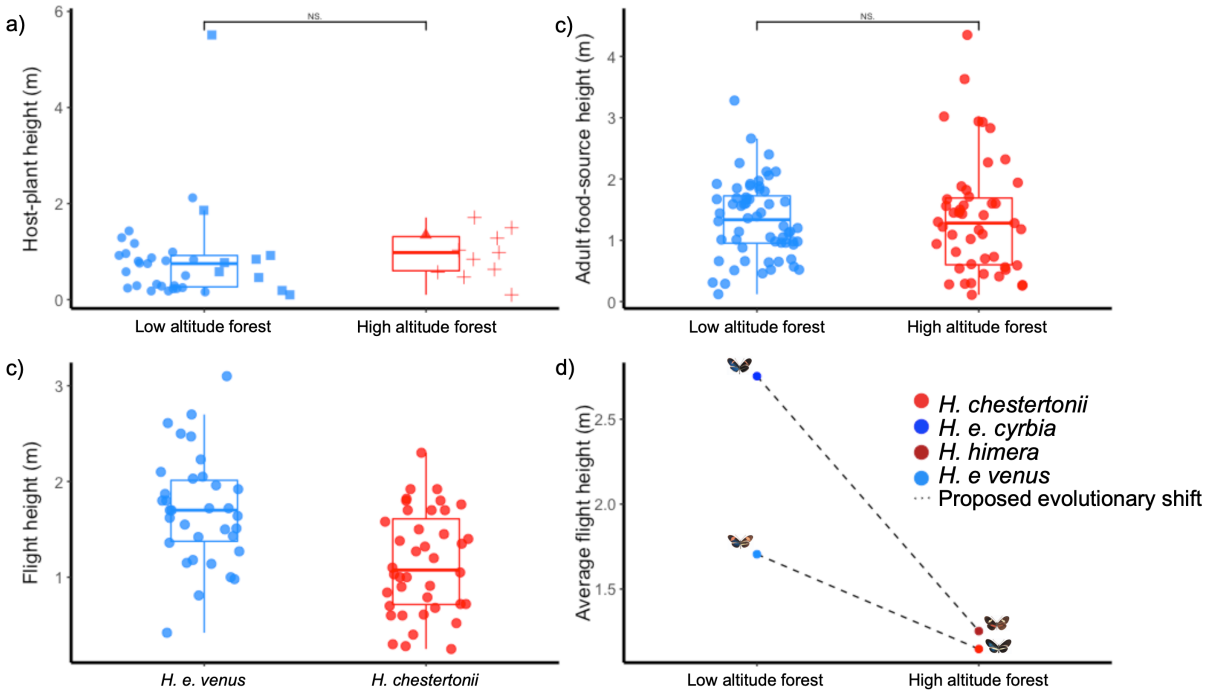

Figure 2. Comparisons in resource distribution and flying-heights in *Heliconius* species. a) Comparison of hostplant heights, b) adult-food source heights, c) flight-height and d) levels of parallelism in flight-height between species from different clines. For a) circles are *Passiflora auriculata*, squares are *P. micropetala*, pluses are *P. suberosa* and triangles *P. biflora*. For a-c) blue *H. e. venus* is blue and *H. chestertonii* is red. For d). *H. e. venus* is blue and *H. chestertonii* is red, *H. e. cyrbia* is dodger blue and *H. himera* is firebrick. Box plots show the median and upper and lower quartiles, each point is an individual measure. Asterisks convey significance levels of comparisons (Wilcoxon test). NS, not significant. * p < 0.05. ** p < 0.01. *** P < 0.001.

Table 1. Semi-partial R2 measures of model terms in models explaining variation in flight-height across *H. himera*, *H. e. cyrbia*, *H. chestertonii* and *H. e. venus*.

	Semi-partial R^2 measures (95% CI)			
Model	**Factor**	**Semi-partial R^2**	**Lower CI**	**Upper CI**
	Habitat	0.451	0.087	0.784
Flight-height~Habitat:Locality	Locality	0.234	0.003	0.661
	Habitat x Locality	0.162	0.001	0.605
Flight-height~Habitat	Habitat	0.546	0.233	0.8

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